

## RESEARCH ARTICLE

# Lower-limb joint mechanics during maximum acceleration sprinting

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## ABSTRACT

We explored how humans adjust the stance phase mechanical function of their major lower-limb joints (hip, knee, ankle) during maximum acceleration sprinting. Experimental data [motion capture and ground reaction force (GRF)] were recorded from eight participants as they performed overground sprinting trials. Six alternative starting locations were used to obtain a dataset that incorporated the majority of the acceleration phase. Experimental data were combined with an inverse-dynamics-based analysis to calculate lower-limb joint mechanical variables. As forward acceleration magnitude decreased, the vertical GRF impulse remained nearly unchanged whereas the net horizontal GRF impulse became smaller as a result of less propulsion and more braking. Mechanical function was adjusted at all three joints, although more dramatic changes were observed at the hip and ankle. The impulse from the ankle plantar-flexor moment was almost always larger than those from the hip and knee extensor moments. Forward acceleration magnitude was linearly related to the impulses from the hip extensor moment ( $R^2=0.45$ ) and the ankle plantar-flexor moment ( $R^2=0.47$ ). Forward acceleration magnitude was also linearly related to the net work done at all three joints, with the ankle displaying the strongest relationship ( $R^2=0.64$ ). The ankle produced the largest amount of positive work ( $1.55\pm 0.17$  J kg<sup>-1</sup>) of all the joints, and provided a significantly greater proportion of the summed amount of lower-limb positive work as running speed increased and forward acceleration magnitude decreased. We conclude that the hip and especially the ankle represent key sources of positive work during the stance phase of maximum acceleration sprinting.

**KEY WORDS:** Propulsion, Impulse, Mechanical work, Hip, Knee, Ankle

## INTRODUCTION

Much of what we know about lower-limb joint mechanics during locomotion in animals and humans has been gleaned from experiments involving constant speed and level ground conditions, neither of which requires a net change in the body's forward kinetic energy. In contrast, the body's forward kinetic energy must be maximised when rapidly accelerating from a stationary position (e.g. animals escaping from a predator; humans competing in a sprint race). Given this energetic requirement, it is

likely that the mechanical function of the lower-limb joints must be adjusted relative to that observed during constant speed locomotion. Which joints (i.e. proximal or distal or both) are mainly responsible for providing the positive work needed to maximise the body's forward kinetic energy? Both animal- and human-based studies have previously considered this question, but as we highlight below there are still many gaps in the existing level of knowledge.

Several studies have investigated joint mechanics during rapid accelerations for a variety of terrestrial animals, including wild turkeys (Roberts and Scales, 2004), tammar wallabies (McGowan et al., 2005) and racing greyhounds (Williams et al., 2009). For bipeds, Roberts and Scales (2004) and McGowan et al. (2005) found that the work required to accelerate the body in a forward direction was predominantly modulated at the ankle and to a lesser degree at the hip. Both studies found positive linear relationships between forward acceleration magnitude and net work done at the hip and ankle. In contrast, for quadrupeds, Williams et al. (2009) found no significant relationship between net work done by the hip and forward acceleration magnitude for either the lead or trail hindlimb, whereas net work done by the stifle (knee) and hock (ankle) were both found to be significantly associated with forward acceleration magnitude for the lead hindlimb. Notwithstanding these differences in joint mechanics during rapid accelerations for bipedal versus quadrupedal locomotion, there are important anatomical and energetic differences among bipeds that may see humans construct joint level mechanics alternatively. We were therefore interested in understanding whether humans behave similarly to other bipedal vertebrates or whether they instead display their own characteristic pattern.

Numerous studies have investigated human lower-limb joint mechanics when maximally accelerating during an overground sprint (Jacobs and van Ingen Schenau, 1992; Johnson and Buckley, 2001; Hunter et al., 2004; Mero et al., 2006; Charalambous et al., 2012; Debaere et al., 2013; Bezodis et al., 2014; Yu et al., 2016; Brazil et al., 2017; Nagahara et al., 2017). Whilst these studies have generated some important insights, they are associated with some noteworthy limitations. Almost all studies reported data for a single discrete region only, such as the initial one to two steps at the start of the sprint (i.e. high forward acceleration magnitude) (Jacobs and van Ingen Schenau, 1992; Mero et al., 2006; Charalambous et al., 2012; Debaere et al., 2013; Bezodis et al., 2014; Brazil et al., 2017) or the mid-region around 12–16 m from the starting location (i.e. medium forward acceleration magnitude) (Johnson and Buckley, 2001; Hunter et al., 2004; Yu et al., 2016). Of these studies, only Yu et al. (2016) included data for more than one region. They compared lower-limb joint moments for the mid- and maximum speed regions (i.e. medium versus low forward acceleration magnitude). Given that the average sprinting speed attained by the participants in the mid-region was already  $7.85\pm 0.61$  m s<sup>-1</sup>, their results do not capture the full extent to which humans may adjust their lower-limb joint mechanics during maximum acceleration sprinting. A recent

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study by Nagahara et al. (2017) addressed this limitation by capturing joint motion data for the entire acceleration phase; however, without force platforms to record ground reaction force (GRF) data, they were limited to calculating lower-limb joint mechanical variables such as moment, power and work for the swing phase only. To our knowledge, equivalent analyses for the stance phase of maximum acceleration sprinting are not available, yet are critical given that forward propulsion of the body can only be instigated during the stance phase. Hence, there is still much to learn about the way humans adjust the mechanical function of their lower-limb joints for generating the necessary positive work to maximise the body's forward kinetic energy when accelerating.

In the present study, we posed the following research question: how do humans modulate the stance phase mechanical function of their major lower-limb joints (hip, knee, ankle) during maximum acceleration sprinting? To address this question, we recorded motion capture and GRF data from eight participants performing repeated sprinting trials. Experimental data were used together with an inverse-dynamics-based analysis to examine a range of variables including trunk and lower-limb joint angles as well as lower-limb joint moments, power and work. We hypothesised that: first, the amount of positive work done by all three lower-limb joints would be greatest when forward acceleration magnitude was maximal (and speed was low), whereas the amount of negative work done by all three lower-limb joints would be greatest when forward acceleration magnitude was minimal (and speed approached steady-state sprinting); and second, based on previous findings for other bipedal vertebrates, hip and ankle joint kinetics (specifically, the impulse of the extensor moment as well as net work done) would display the strongest positive relationships with forward acceleration magnitude.

## MATERIALS AND METHODS

### Participants

A total of eight participants (5 men and 3 women) were voluntarily recruited and provided written, informed consent in accordance with the requirements of the Human Research Ethics Committee at The University of Melbourne. All participants were sub-elite track and field athletes. None of the participants were suffering from a musculoskeletal injury at the time of testing. The anthropometric composition of the cohort was as follows: age  $24.3 \pm 5.1$  years; height  $177.2 \pm 7.9$  cm; and body mass  $70.4 \pm 8.1$  kg.

### Experimental setup

Data were recorded at the Australian Institute of Sport, Bruce, ACT, Australia. Participants were required to perform repeated maximum acceleration sprinting trials on an indoor 110 m synthetic running track. Eight large ( $900 \times 600$  mm<sup>2</sup>) force plates (Kistler Instrument Corp., Amherst, NY, USA) were used to record GRF data at a sampling rate of 1500 Hz. The force plates were embedded in the laboratory floor immediately adjacent to each other and were covered with the same synthetic material as the running track. This arrangement provided a segment of  $\sim 7.2$  m (i.e.  $8 \times 900$  mm) in the running track where GRF data could be recorded. A 22-camera 3D motion analysis system (VICON, Oxford Metrics Ltd, Oxford, UK) was positioned on both sides of the running track surrounding the force plates and was used to record the trajectories of small (14 mm) retro-reflective skin-mounted markers at a sampling rate of 250 Hz.

### Experimental protocol

Participants wore their usual sprinting spikes during the experiment. Markers were placed at various anatomical locations on the trunk,

pelvis and both lower limbs. For the trunk, a single marker was placed over the seventh cervical spinous process (C7 marker). For the pelvis, markers were placed over the most prominent aspect of both anterior superior iliac spines. Participants also wore a pelvic strap, which contained a small thermoplastic triangular plate with four permanently fixed markers. The plate was mounted directly over the sacrum such that the middle superior marker on the plate was overlying the midpoint between both posterior superior iliac spines (SACR marker). For the thigh and shank, anatomical markers were mounted over the medial and lateral femoral condyles and the medial and lateral malleoli. Three tracking markers were placed over the anterolateral aspect of the thigh as well as the middle third of the shank. For the foot, markers were placed on the outer sole of the spikes over the inferior and superior end of a line bisecting the heel, the medial and lateral part of the dorsal surface of the midfoot, and the toe region overlying the junction between the second and third metatarsophalangeal joints. To define anatomical reference frames, an initial static trial was collected with the participant standing in the middle of the calibrated measurement volume with all markers *in situ*. Medial femoral condyle and medial malleoli markers were removed before commencing the dynamic trials.

All participants were allowed to follow their usual warm-up routine. Participants performed numerous maximum acceleration sprinting trials, starting at a variety of incremental distances from the centre of the calibrated measurement volume. A three-point crouched starting pose without blocks was used by all participants for all trials. The participant's non-dominant leg was the front leg in the starting pose. A total of six different starting locations on the running track were identified per participant. The initial starting location was within the calibrated measurement volume such that the 1st foot contact (i.e. first step for the participant's dominant leg) occurred in the middle of the first force plate. The next starting location was  $\sim 6$  m back from the initial starting location, just outside the boundary of the calibrated measurement volume. A distance of  $\sim 6$  m separated each of the six different starting locations, such that the final starting location was at least 30 m away from the initial starting location. This incremental process allowed us to record experimental data for as many successive foot contacts as possible for each lower limb throughout the initial  $\sim 40$  m section of maximum acceleration sprinting (albeit via separate trials). Participants commenced all trials following a verbal cue from the tester. They self-selected their required recovery time between trials such that a constant maximal effort was achieved for every trial. Most participants were only capable of completing one trial per start location without risking fatigue.

### Data analysis

For each participant, stance phase experimental data for an arbitrarily selected single lower limb were extracted for further analysis. A valid foot contact occurred when the entire foot landed within the boundaries of a single force plate. Stance phase was defined by the events of foot-strike and toe-off, which were identified from the raw GRF data. All available trials were carefully reviewed and a single trial per start location was selected for further analysis for each participant. From these trials, we successfully extracted 10 valid foot contacts from a single lower limb for five participants: the dominant limb for four participants and the non-dominant limb for one participant. Nine valid foot contacts were successfully extracted from the dominant lower limb for the remaining three participants.

Before calculating joint angles and moments, we filtered the GRF and marker trajectories using a fourth-order (zero lag) low-pass

Butterworth filter (Winter, 2009) with a cut-off frequency of 10 Hz. These data were filtered with the same cut-off frequency to avoid the issue of impact artifacts in the joint moments (Bisseling and Hof, 2006; Kristianslund et al., 2012). An eight-segment biomechanical model (trunk, pelvis, left/right thigh, left/right shank, left/right foot) implemented in Bodybuilder software (VICON, Oxford Metrics Ltd, Oxford, UK) was used to calculate joint angles and net joint moments. The structure of the model was essentially the same as that used previously (Schache et al., 2011). For the purposes of the present study, the model included an additional trunk segment to measure forward trunk inclination, which was defined as the angle between the laboratory (global) vertical axis and a line connecting the SACR and C7 markers measured in the sagittal plane of the laboratory (global) reference frame. Hip, knee and ankle joint angles were calculated using a joint coordinate system convention as has been previously described (Schache and Baker, 2007). The internal hip, knee and ankle joint moments were calculated using a standard inverse-dynamics analysis (Winter, 2009). Inertial properties for each segment were estimated using equations based on segment length and body mass (de Leva, 1996). The net joint moment was expressed in the same non-orthogonal joint coordinate system used to calculate joint angles (Schache and Baker, 2007). Joint moment data were normalised to body mass ( $\text{N m kg}^{-1}$ ). The net power at each lower-limb joint was determined by taking the product of the net joint moment and joint angular velocity. Joint power data were also normalised to body mass ( $\text{W kg}^{-1}$ ). Normalised net joint power data were integrated over the duration of the stance phase to calculate the work done ( $\text{J kg}^{-1}$ ). All periods of positive and negative work were summed independently to determine the total amount of positive and negative work done by a given joint across the stance phase. Net work done by a given joint was also calculated by taking the sum of the total amount of positive and negative work done.

For the purposes of data analysis, we defined three acceleration conditions (high, medium, low). Each condition represented a different region of maximum acceleration sprinting based on the magnitude of the average forward acceleration of the body's centre of mass. This analytical approach was based on that previously utilised by Williams et al. (2009) to quantify hindlimb mechanics in racing greyhounds when accelerating. The magnitude of the average forward acceleration of the body's centre of mass for a given foot contact was calculated by taking the average of the raw fore-aft (horizontal) GRF over the duration of the stance phase and dividing it by the participant's body mass. We selected data for a single foot contact for each of the three acceleration conditions per participant. The 'high' acceleration condition included data for a foot contact that occurred close to when participants started sprinting, whereas the 'low' acceleration condition included data for a foot contact that occurred close to when participants were approaching their maximum sprinting speed. The 'medium' acceleration condition included data for a foot contact that occurred mid-way between these two extremes. The corresponding speed achieved for each acceleration condition was determined by calculating the average forward velocity of the SACR marker across the stance phase for the selected foot contact.

We compared outcome measures of interest both qualitatively and quantitatively across the three acceleration conditions. The qualitative analysis involved generating time-series plots. Data for each participant were time normalised as a percentage (0–100%) of stance phase and then averaged across participants to generate mean curves for each acceleration condition. The quantitative analysis involved selecting key discrete variables and calculating mean

( $\pm 1$  s.d.) magnitude for these variables for each acceleration condition. Numerous discrete variables were calculated from the raw GRF [normalised to body weight (BW)]. These variables were chosen based on those used in previous studies and included: (a) the peak magnitude of the vertical GRF as well as the peak magnitude of the negative (braking) and positive (propulsive) components of the horizontal GRF; (b) the impulse (integral over time) of the vertical GRF, the net impulse of the horizontal GRF, and the impulse of each component of the horizontal GRF calculated separately, i.e. the negative (braking) and positive (propulsive) components; (c) the effective impulse of the vertical GRF, i.e. the product of the stance phase duration and the vertical GRF applied in excess of BW (Weyand et al., 2000, 2010); (d) the ratio of forces (%), i.e. the ratio of the horizontal GRF to the total GRF (resultant of the force vectors measured on the  $x$ -,  $y$ - and  $z$ -axes) calculated instantaneously and then averaged across the stance phase (Rabita et al., 2015); and (e) the ratio of impulses (%), i.e. the net impulse of the horizontal GRF divided by the impulse of the vertical GRF. Numerous discrete variables were also calculated from the joint kinematic and kinetic data. These variables included: (a) the mean angle of trunk forward inclination across the stance phase as well as the sagittal plane hip, knee and ankle joint angles at foot-strike and toe-off; (b) the peak magnitude and impulse (integral over time) for the sagittal plane hip, knee and ankle joint moments (positive and negative portions separately); and (c) net work done by the hip, knee and ankle joints across the stance phase as well as the total amount of positive and negative work done by each joint (expressed in absolute units and as a percentage of the summed amount of positive or negative work done by the lower-limb joints, respectively).

### Statistical analysis

Statistical analysis was conducted using IBM SPSS Statistics version 25 (IBM Corporation, Armonk, NY, USA). One-way repeated-measures ANOVA tests were used to determine whether lower-limb joint mechanical variables were significantly different when comparing acceleration conditions (high, medium, low). Effect size was estimated using partial  $\eta^2$ . If a significant main effect was found, *post hoc* paired  $t$ -tests were used to determine which acceleration conditions were significantly different from each other. Because of the substantial number of statistical comparisons, a conservative level of significance was set at  $P < 0.01$ . We also explored the relationship between the forward acceleration magnitude and: (a) the ratio of impulses (%); (b) the impulse magnitudes of all the positive extensor moments; and (c) the net work done at each of the lower-limb joints. Linear regression equations were fitted to the scatterplots and the coefficient of determination ( $R^2$ ) was used to describe the strength of the relationship. In the present study,  $R^2 > 0.26$  was considered 'strong';  $0.13 < R^2 < 0.26$ , 'medium'; and  $R^2 < 0.12$ , 'weak'.

### RESULTS

Forward acceleration magnitude significantly differed across the three acceleration conditions ( $P < 0.001$ , all comparisons). Data for the high acceleration condition were obtained from the 1st foot contact ( $N=7$ ) and 2nd foot contact ( $N=1$ ). Forward acceleration magnitude for this condition ranged from 4.66 to 6.15  $\text{m s}^{-2}$ , with a mean  $\pm 1$  s.d. of 5.30  $\pm 0.64$   $\text{m s}^{-2}$ . Speed ranged from 3.55 to 5.04  $\text{m s}^{-1}$ , with a mean  $\pm 1$  s.d. of 3.92  $\pm 0.49$   $\text{m s}^{-1}$ . Stance time ranged from 0.161 to 0.233 s, with a mean  $\pm 1$  s.d. of 0.189  $\pm 0.029$  s. Data for the medium acceleration condition were obtained from the 5th foot contact ( $N=3$ ), 7th foot contact ( $N=3$ ), 8th foot

contact ( $N=1$ ) and 9th foot contact ( $N=1$ ). Forward acceleration magnitude for this condition ranged from 2.71 to 3.10  $\text{m s}^{-2}$ , with a mean $\pm$ 1 s.d. of  $2.93\pm 0.14 \text{ m s}^{-2}$ . Speed ranged from 6.22 to 8.46  $\text{m s}^{-1}$ , with a mean $\pm$ 1 s.d. of  $7.29\pm 0.93 \text{ m s}^{-1}$ . Stance time ranged from 0.117 to 0.159 s, with a mean $\pm$ 1 s.d. of  $0.131\pm 0.015 \text{ s}$ . Data for the low acceleration condition were obtained from the 17th foot contact ( $N=2$ ), 19th foot contact ( $N=5$ ) and 22nd foot contact ( $N=1$ ). Forward acceleration magnitude for this condition ranged from 1.23 to 1.58  $\text{m s}^{-2}$ , with a mean $\pm$ 1 s.d. of  $1.32\pm 0.11 \text{ m s}^{-2}$ . Speed ranged from 7.84 to 10.24  $\text{m s}^{-1}$ , with a mean $\pm$ 1 s.d. of  $9.14\pm 0.88 \text{ m s}^{-1}$ . Stance time ranged from 0.098 to 0.124 s, with a mean $\pm$ 1 s.d. of  $0.111\pm 0.010 \text{ s}$ .

### GRF and impulse

The profile of both the vertical and the horizontal GRF differed across the three acceleration conditions (Fig. 1). For example, the size of the negative (braking) component of the horizontal GRF increased as forward acceleration magnitude decreased, whereas the size of the positive (propulsive) component decreased. A significant main effect for acceleration condition was found for all discrete GRF variables, with the exception of the total impulse of the vertical GRF (Table 1).

As forward acceleration magnitude decreased, the peak of the vertical GRF increased in magnitude but the total impulse did not change (Table 1). The magnitude of the peak vertical GRF was significantly different between all three acceleration conditions ( $P\leq 0.008$ , all comparisons). The average magnitude of the peak vertical GRF was 71% greater for the low compared with the high acceleration condition. The total impulse of the vertical GRF remained constant across all three acceleration conditions, whereas a significant main effect for acceleration condition was found for the effective impulse of the vertical GRF. Specifically, the effective impulse of the vertical GRF was significantly greater for the medium and low acceleration conditions compared with the high acceleration condition ( $P<0.001$ , both cases), with no significant difference between the medium and low acceleration conditions ( $P=0.114$ ).

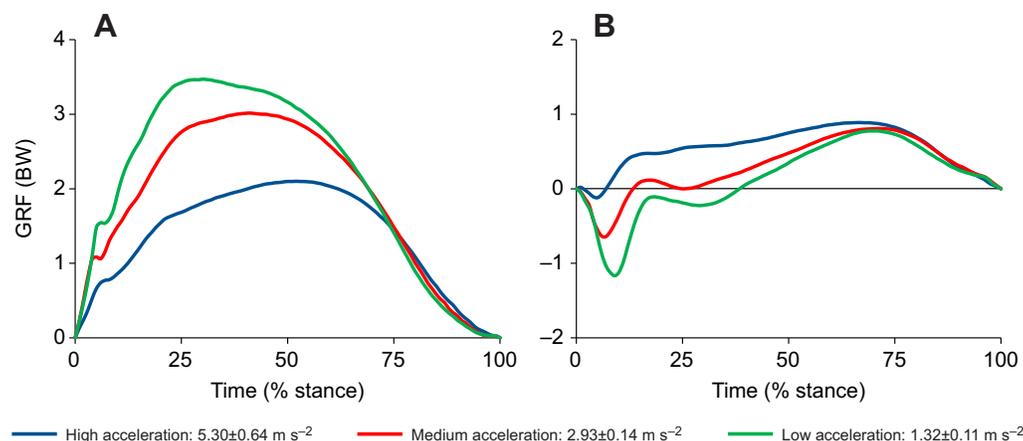
Both the peak and the impulse of the braking component of the horizontal GRF were significantly different between all three acceleration conditions ( $P\leq 0.003$ , all comparisons). There was a 6.9- and 13.3-fold increase in the absolute average magnitude of the peak and impulse of the braking component, respectively, for the

low compared with the high acceleration condition (Table 1). A significant main effect for acceleration condition was also found for the peak and impulse of the propulsive component. Specifically, the peak of the propulsive component was significantly greater for the high acceleration condition compared with the medium and low acceleration conditions ( $P\leq 0.005$ , both comparisons), with no significant difference found between the medium and low acceleration conditions ( $P=0.048$ ). The impulse of the propulsive component was significantly different between all three acceleration conditions ( $P<0.001$ , all comparisons). The average magnitude of the propulsive impulse decreased by 71% for the low compared with the high acceleration condition.

The net horizontal GRF represented a progressively smaller proportion of the total or vertical GRF as forward acceleration magnitude decreased. This result is evidenced by the significant main effects for acceleration condition on both the ratio of forces and the ratio of impulses (Table 1). Both variables were found to be significantly different between all three acceleration conditions ( $P<0.001$ , all comparisons). Furthermore, the ratio of impulses displayed a strong linear relationship with forward acceleration magnitude ( $P<0.001$ ) (Fig. 2).

### Sagittal plane trunk and lower-limb joint angles

As forward acceleration magnitude decreased, the profiles of the trunk, hip and ankle angles during stance remained similar in shape but were progressively offset towards reduced forward inclination, flexion and dorsiflexion, respectively (Fig. 3). However, the profile of the knee joint angle did display a change in shape, most evident during early stance. The knee extended consistently throughout stance for the high acceleration condition, whereas the knee flexed during the first half of stance and then extended during the second half of stance for the low acceleration condition. A significant main effect for acceleration condition was found for all kinematic variables, with the exception of the knee joint angle at toe-off (Table 2). The most notable effects involved the mean angle of forward trunk inclination during stance as well as the hip, knee and ankle angles at foot-strike, where significant differences were present between all three acceleration conditions ( $P\leq 0.008$ , all comparisons). Specifically, as forward acceleration magnitude decreased, the trunk gradually became more upright during stance, the hip and knee became less flexed at foot-strike, and the ankle became more plantar-flexed at foot-strike.



**Fig. 1. Group mean ground reaction force (GRF) curves plotted across stance phase for the three acceleration conditions.** GRF data were normalised to body weight (BW). Stance phase was time normalised from 0% (foot strike) to 100% (toe-off). (A) The vertical GRF component. (B) The horizontal GRF component, where positive represents propulsion and negative represents braking.

**Table 1. Discrete ground reaction force variables**

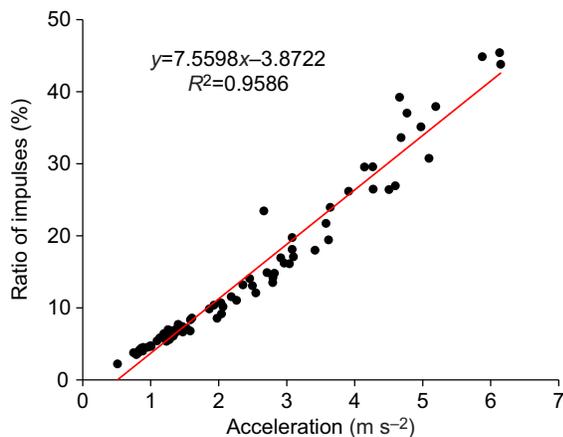
Variable	Acceleration condition			Effect size (partial $\eta^2$ )
	High	Medium	Low	
Peak vGRF (BW)*	2.13±0.19 <sup>2,3</sup>	3.04±0.28 <sup>1,3</sup>	3.63±0.53 <sup>1,2</sup>	0.882
Total impulse vGRF (BW s)	0.26±0.03	0.25±0.03	0.23±0.01	0.317
Effective impulse vGRF (BW s)*	0.07±0.01 <sup>2,3</sup>	0.12±0.01 <sup>1</sup>	0.12±0.01 <sup>1</sup>	0.913
Peak negative (braking) hGRF (BW)*	-0.17±0.17 <sup>2,3</sup>	-0.73±0.36 <sup>1,3</sup>	-1.20±0.18 <sup>1,2</sup>	0.906
Impulse negative (braking) hGRF (BW s)*	-0.00±0.00 <sup>2,3</sup>	-0.01±0.00 <sup>1,3</sup>	0.02±0.00 <sup>1,2</sup>	0.972
Peak positive (propulsive) hGRF (BW)*	0.90±0.11 <sup>2,3</sup>	0.82±0.07 <sup>1</sup>	0.78±0.06 <sup>1</sup>	0.731
Impulse positive (propulsive) hGRF (BW s)*	0.10±0.01 <sup>2,3</sup>	0.05±0.00 <sup>1,3</sup>	0.03±0.00 <sup>1,2</sup>	0.984
Ratio of forces (%)*	36.99±4.39 <sup>2,3</sup>	23.17±1.30 <sup>1,3</sup>	17.22±2.00 <sup>1,2</sup>	0.934
Ratio of impulses (%)*	39.48±4.51 <sup>2,3</sup>	15.87±1.48 <sup>1,3</sup>	6.35±0.46 <sup>1,2</sup>	0.977

Asterisks indicate variables where a significant main effect for acceleration condition was found ( $P<0.01$ ). <sup>1</sup>Significant difference compared with the high acceleration condition. <sup>2</sup>Significant difference compared with the medium acceleration condition. <sup>3</sup>Significant difference compared with the low acceleration condition.

vGRF, vertical ground reaction force; hGRF, horizontal ground reaction force; BW, body weight.

### Sagittal plane lower-limb joint moments

Overall, only the profile for the hip joint moment demonstrated an obvious change in shape, with the switch from a positive (extensor) to negative (flexor) moment occurring later in stance for the high acceleration condition compared with the medium and low acceleration conditions (Fig. 4A). A significant main effect for acceleration condition was found for the impulse of the hip extensor moment (Table 2). Compared with the high acceleration condition, the average impulse of the hip extensor moment was significantly lower for both the medium and low acceleration conditions ( $P\leq 0.004$ , both comparisons), with no significant difference between the medium and low acceleration conditions ( $P=0.013$ ). A significant main effect was also found for the impulse of the ankle plantar-flexor moment. The average impulse of the ankle plantar-flexor moment was largest for the high acceleration condition and smallest for the low acceleration condition. It was significantly different between all three conditions ( $P\leq 0.009$ , all comparisons). Strong linear relationships were found between forward acceleration magnitude and the impulse of the hip extensor moment as well as the impulse of the ankle plantar-flexor moment ( $P<0.001$ , both cases). The two variables displayed a gradient of a similar magnitude (Fig. 5). No relationship was found between forward acceleration magnitude and the impulse of the knee extensor moment ( $P=0.738$ ).



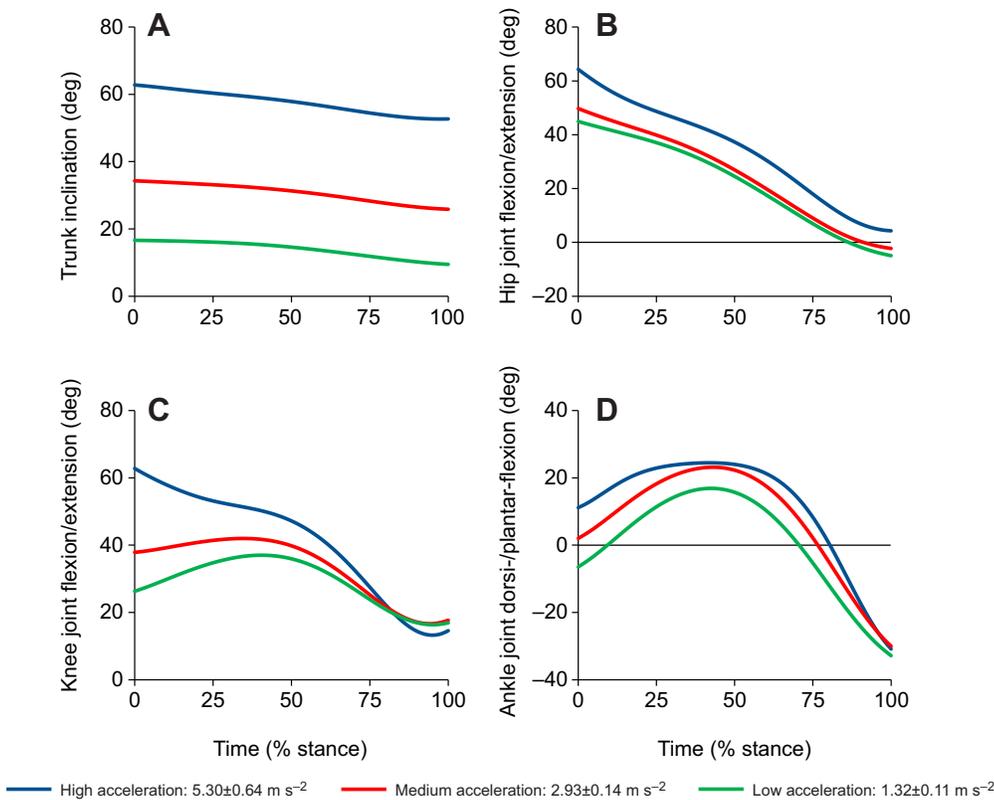
**Fig. 2. The ratio of impulses versus forward acceleration magnitude.** The ratio was calculated by dividing the net impulse of the horizontal GRF by the impulse of the vertical GRF for each foot contact for a single lower-limb for every participant (circles). The red line shows the best-fit linear regression describing the relationship between forward acceleration magnitude ( $x$ ) and the ratio of impulses ( $y$ ).

### Lower-limb joint power and work

The summed amount of lower-limb joint power versus time for the three acceleration conditions is plotted in Fig. S1. Power absorption appeared to be affected more than power generation with a change in forward acceleration magnitude (Fig. 6). Specifically, peak power generation at the hip and knee remained of a similar magnitude across all three acceleration conditions, whereas peak power generation at the ankle was of an equivalent magnitude for the medium and low acceleration conditions but was lower for the high acceleration condition. In contrast, peak power absorption was observed to increase in magnitude at all three joints as forward acceleration magnitude decreased. The amount of positive work was largest for the high acceleration condition and smallest for the low acceleration condition for all three joints, whereas the opposite was true for the amount of negative work (Table 2). A significant main effect for acceleration condition was found for positive, negative and net work done by the hip, net work done by the knee, as well as negative and net work done by the ankle (Table 2). Only net work done by the ankle was significantly different between all three acceleration conditions ( $P\leq 0.007$ , all comparisons). Strong linear relationships were observed between net work done and forward acceleration magnitude for all three joints ( $P<0.001$ , all cases). Net work done by the hip and ankle had a slope of a similar magnitude ( $\sim 0.2$ ), whereas net work done by the knee had a more gradual slope of 0.1 (Fig. 7).

The summed amount of positive work done by the lower limb became progressively smaller as forward acceleration magnitude decreased (Fig. 8, top). Moreover, a proximal to distal shift tended to occur in the proportional contributions from each joint to the summed amount of positive work done by the lower limb as forward acceleration magnitude decreased. For example, the average proportional contribution from the hip was largest for the high acceleration condition (29.1%) and smallest for the low acceleration condition (22.7%), whereas the average proportional contribution from the ankle displayed the opposite effect, being smallest for the high acceleration condition (50.0%) and largest for the low acceleration condition (60.8%). A significant main effect was only found for the proportional contribution from the ankle. Specifically, the proportional contribution from the ankle to the summed amount of positive work done by the lower limb was significantly larger for the medium and low acceleration conditions compared with the high acceleration condition ( $P\leq 0.008$ , both comparisons).

The summed amount of negative work done by the lower limb became progressively larger as forward acceleration magnitude



**Fig. 3. Group mean sagittal plane trunk and lower-limb joint angles plotted across the stance phase for the three acceleration conditions.** Stance phase was time normalised from 0% (foot-strike) to 100% (toe-off). (A) The angle between the trunk and the vertical (i.e. forward trunk inclination). (B) The hip joint angle (flexion is positive; extension is negative). (C) The knee joint angle (flexion is positive; extension is negative). (D) The ankle joint angle [0 deg represents the neutral position (i.e. plantar-grade); dorsi-flexion is positive; plantar-flexion is negative].

decreased (Fig. 8, bottom). The proportional contributions from the hip, knee and ankle to the summed amount of negative work done by the lower limb were not found to significantly differ across the three acceleration conditions. Thus, the increase in the amount of negative work done by the lower limb as forward acceleration magnitude decreased was evenly distributed across all three joints.

## DISCUSSION

The present study tested two hypotheses: first, the amount of positive work done by all three lower-limb joints would be greatest when forward acceleration magnitude was maximal, whereas the amount of negative work done by all three lower-limb joints would be greatest when forward acceleration magnitude was minimal; and second, hip and ankle joint kinetics would display the strongest positive relationships with forward acceleration magnitude. Our first hypothesis is concisely summarised by data contained in Fig. 8, where the summed amount of positive work done by the lower limb became less (i.e. the area of the circle was smaller) as forward acceleration magnitude decreased, whilst the opposite effect occurred for the summed amount of negative work done by the lower limb. Our second hypothesis is perhaps best supported by data contained in Fig. 5, where strong positive linear relationships were found to exist between forward acceleration magnitude and the impulse of the positive extensor moments at the hip and ankle. In the sections below, we discuss our major findings in further detail.

### Human lower-limb joint mechanics during the stance phase of maximal acceleration sprinting

Mechanical function was adjusted at all three joints to some extent. For example, the profile of the joint power curve was noticeably influenced by acceleration condition for the hip, knee and ankle (Fig. 6). Also, the amount of net work done by the hip, knee and ankle became significantly less as forward acceleration magnitude

decreased (Table 2). Nevertheless, when considering all of the available evidence from the present study, maximum acceleration sprinting would appear to be particularly dependent on the performance of the hip and ankle, with the ankle arguably being most critical. This premise is based on the following key observations. First, the impulse of the ankle plantar-flexor moment was almost always greater than the impulse of the positive extensor moment at the hip and the knee irrespective of forward acceleration magnitude (Fig. 5). Second, net work done by the ankle displayed the strongest association with forward acceleration magnitude (Fig. 7). Third, whilst the amount of positive work done by all of the joints declined as forward acceleration magnitude decreased (and speed increased), the decline in positive work was not uniformly distributed across the hip, knee and ankle. Positive work done by the ankle appeared to be relatively preserved; for example, positive work done by the hip and knee decreased by ~50% for the low compared with the high acceleration condition, whereas positive work done by the ankle showed virtually no change between the high and medium acceleration conditions (~1.5 J kg<sup>-1</sup>) and only decreased by ~20% for the low compared with the medium acceleration condition (Table 2). Hence, we observed a significant increase in the proportional contribution from the ankle to the summed amount of positive work done by the lower limb as forward acceleration magnitude decreased (Fig. 8, top). When interpreted together, our observations provide some clues about the importance of ankle joint mechanics during maximum acceleration sprinting. This suggestion is consistent with previous musculoskeletal modelling studies that have found the ankle plantar-flexor muscles to produce the largest contribution of all the major lower-limb muscles towards the vertical and forward acceleration of the body's centre of mass during the stance phase of sprinting (Dorn et al., 2012; Debaere et al., 2015). It is also consistent with previous studies linking sprinting ability in humans

**Table 2. Joint kinematic and kinetic variables**

Variable	Acceleration condition			Effect size (partial $\eta^2$ )
	High	Medium	Low	
<b>Angle</b>				
Mean forward trunk inclination (deg)*	57.56±7.97 <sup>2,3</sup>	30.68±4.76 <sup>1,3</sup>	13.88±4.50 <sup>1,2</sup>	0.966
Hip joint angle at foot-strike (deg)*	64.29±6.14 <sup>2,3</sup>	49.72±3.73 <sup>1,3</sup>	44.91±3.91 <sup>1,2</sup>	0.922
Hip joint angle at toe-off (deg)*	4.30±6.94 <sup>2,3</sup>	-2.26±6.13 <sup>1</sup>	-4.93±5.64 <sup>1</sup>	0.769
Knee joint angle at foot-strike (deg)*	62.80±8.48 <sup>2,3</sup>	37.86±4.70 <sup>1,3</sup>	26.29±4.70 <sup>1,2</sup>	0.943
Knee joint angle at toe-off (deg)	14.57±9.67	17.69±8.43	16.90±5.37	0.146
Ankle joint angle at foot-strike (deg)*	11.16±5.02 <sup>2,3</sup>	2.02±4.65 <sup>1,3</sup>	-6.46±3.64 <sup>1,2</sup>	0.870
Peak ankle joint angle during stance (deg)*	24.90±4.23 <sup>3</sup>	23.26±3.44 <sup>3</sup>	16.91±3.49 <sup>1,2</sup>	0.597
Ankle joint angle at toe-off (deg)*	-30.86±4.41	-30.02±2.81 <sup>3</sup>	-32.85±3.36 <sup>2</sup>	0.500
<b>Moment</b>				
Peak hip extensor moment (N m kg <sup>-1</sup> )	2.21±0.49	2.21±0.69	2.64±0.87	0.358
Hip extensor moment impulse (N m (kg s <sup>-1</sup> ))*	0.18±0.06 <sup>2,3</sup>	0.10±0.04 <sup>1</sup>	0.0.9±0.03 <sup>1</sup>	0.682
Peak hip flexor moment (N m kg <sup>-1</sup> )	-2.81±0.78	-2.52±0.71	-2.29±0.69	0.176
Hip flexor moment impulse (N m kg <sup>-1</sup> s <sup>-1</sup> )	-0.09±0.03	-0.10±0.03	-0.10±0.03	0.096
Peak knee extensor moment (N m kg <sup>-1</sup> )	1.63±0.59	2.27±0.54	2.47±0.54	0.396
Knee extensor moment impulse (N m kg <sup>-1</sup> s <sup>-1</sup> )	0.16±0.08	0.14±0.05	0.13±0.04	0.075
Peak ankle plantar-flexor moment (N m kg <sup>-1</sup> )	3.20±0.34	3.68±0.43	3.56±0.60	0.287
Ankle plantar-flexor moment impulse (N m kg <sup>-1</sup> s <sup>-1</sup> )*	0.38±0.04 <sup>2,3</sup>	0.29±0.04 <sup>1,3</sup>	0.23±0.03 <sup>1,2</sup>	0.864
<b>Work</b>				
Hip joint positive work (J kg <sup>-1</sup> )*	0.93±0.41	0.66±0.26	0.50±0.23	0.543
Hip joint negative work (J kg <sup>-1</sup> )*	-0.45±0.17 <sup>3</sup>	-0.61±0.20	-0.79±0.19 <sup>1</sup>	0.599
Hip joint net work (J kg <sup>-1</sup> )*	0.48±0.52 <sup>3</sup>	0.05±0.25 <sup>3</sup>	-0.29±0.25 <sup>2,3</sup>	0.693
Knee joint positive work (J kg <sup>-1</sup> )	0.65±0.30	0.42±0.08	0.35±0.19	0.439
Knee joint negative work (J kg <sup>-1</sup> )	-0.09±0.06	-0.16±0.06	-0.30±0.19	0.474
Knee joint net work (J kg <sup>-1</sup> )*	0.56±0.34 <sup>3</sup>	0.26±0.12	0.05±0.29 <sup>1</sup>	0.581
Ankle joint positive work (J kg <sup>-1</sup> )	1.55±0.17	1.52±0.22	1.28±0.22	0.424
Ankle joint negative work (J kg <sup>-1</sup> )*	-0.35±0.15 <sup>2,3</sup>	-0.73±0.17 <sup>1</sup>	-0.87±0.19 <sup>1</sup>	0.756
Ankle joint net work (J kg <sup>-1</sup> )*	1.19±0.14 <sup>2,3</sup>	0.79±0.20 <sup>1,3</sup>	0.41±0.14 <sup>1,2</sup>	0.867

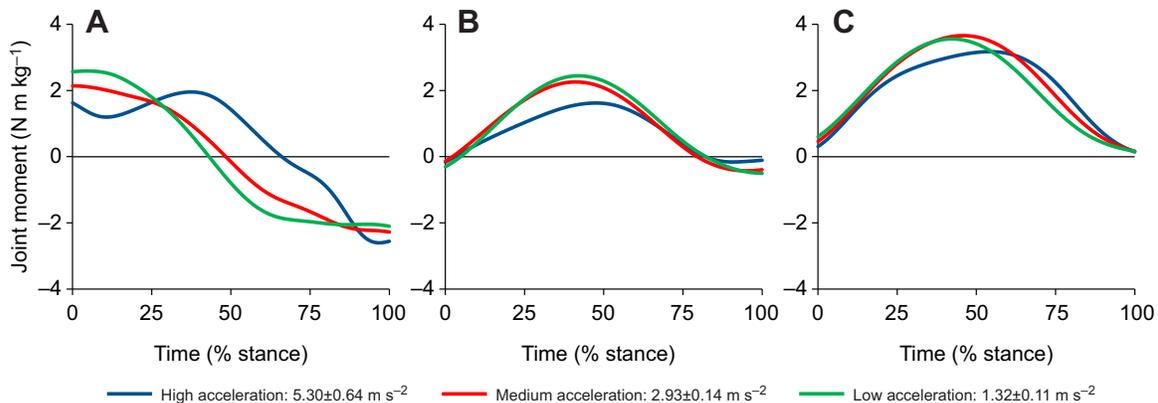
Asterisks indicate variables where a significant main effect for acceleration condition was found ( $P<0.01$ ). <sup>1</sup>Significant difference compared with the high acceleration condition. <sup>2</sup>Significant difference compared with the medium acceleration condition. <sup>3</sup>Significant difference compared with the low acceleration condition.

NB: a significant main effect for acceleration condition was found for hip joint positive work ( $P=0.004$ ) but none of the *post hoc* paired *t*-tests were found to be significant ( $P\geq 0.12$ , all comparisons).

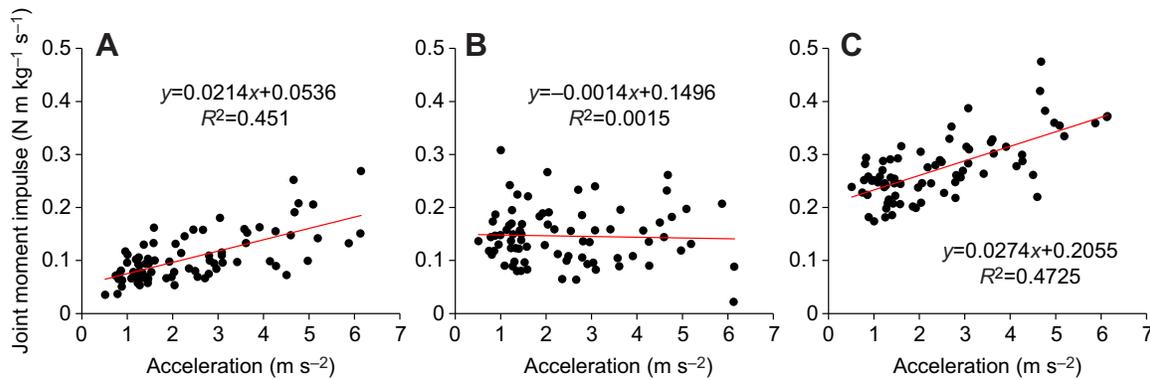
with ankle plantar-flexor properties, such as a smaller Achilles tendon moment arm and longer muscle fascicles (Lee and Piazza, 2009; Baxter et al., 2012).

In a recent study, Matsuo et al. (2019) measured GRF data from 12 male athletes for every step continuously over the whole acceleration stage of sprint running (i.e. over 50 m from the start). Using these data, the external mechanical work done was calculated for each step. They found the total external mechanical work done

during the braking phase of the step to increase by at least 4.6-fold over the whole acceleration stage, whereas the external mechanical work done during the propulsive phase only decreased by 0.47-fold (53%). We observed a similar phenomenon in the present study. Whilst the summed amount of positive work done by the lower limb always exceeded the summed amount of negative work done irrespective of acceleration condition (Fig. 8), a noteworthy observation was that the rise in power absorption and negative



**Fig. 4. Group mean sagittal plane lower-limb joint moments plotted across stance phase for the three acceleration conditions.** Joint moment data were normalised to body mass. Stance phase was time normalised from 0% (foot strike) to 100% (toe-off). (A) The 'internal' hip joint moment (extensor is positive; flexor is negative). (B) The 'internal' knee joint moment (extensor is positive; flexor is negative). (C) The 'internal' ankle joint moment (plantar-flexor is positive; dorsi-flexor is negative).

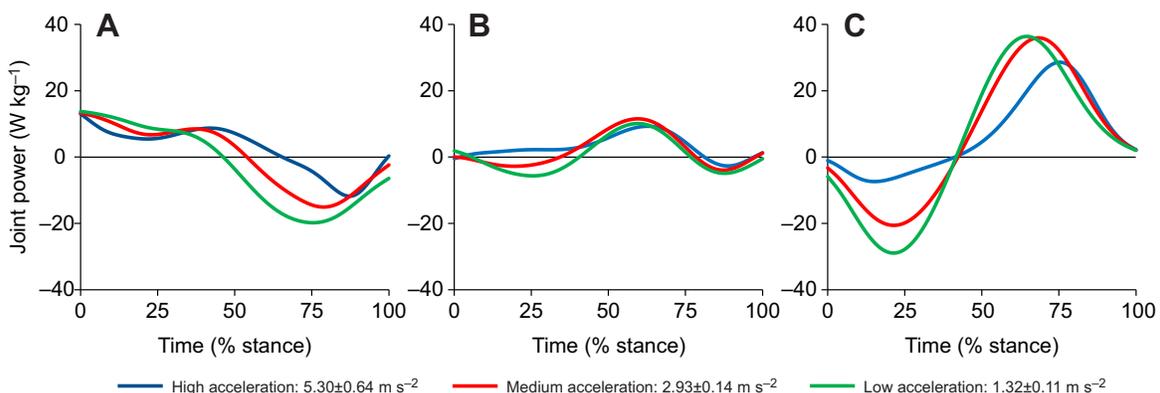


**Fig. 5. The impulse (integral over time) of the positive portion of the sagittal plane lower-limb joint moments versus forward acceleration magnitude.** The circles represent data for each foot contact for a single lower limb for all participants ( $N=77$  foot contacts analysed in total). (A) The positive (extensor) impulse of the hip joint moment. (B) The positive (extensor) impulse of the knee joint moment. (C) The positive (plantar-flexor) impulse of the ankle joint moment. The red lines show best-fit linear regressions describing the relationship between forward acceleration magnitude ( $x$ ) and the positive impulse of the joint moment ( $y$ ).

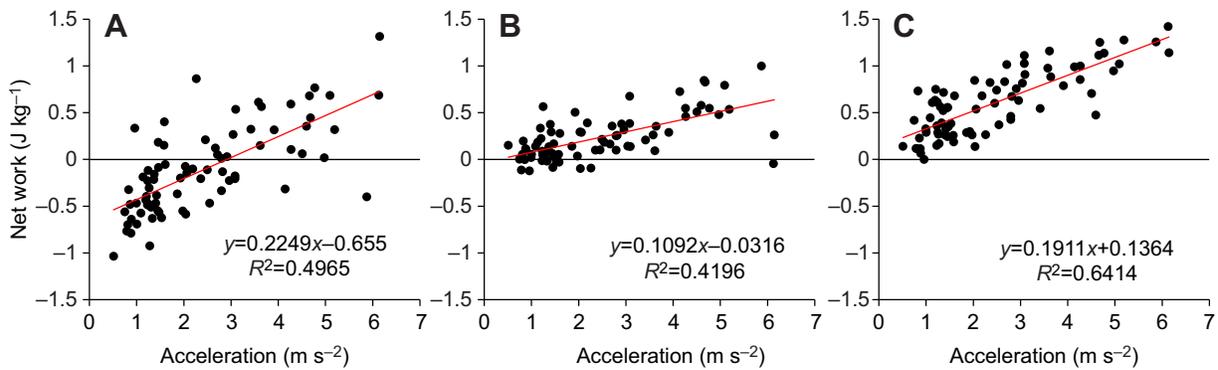
work done as forward acceleration magnitude decreased appeared to be more substantial than the concomitant fall in power generation and positive work done. For example, for the low compared with the high acceleration condition, the summed amount of negative work done by the lower limb was increased by 2.2-fold, whereas the summed amount of positive work done by the lower limb was only decreased by 0.68-fold (or  $\sim 30\%$ ). When inspecting the joint power curves in Fig. 6 (and data contained in Table 2), it is obvious that the bulk of the rise in power absorption and negative work done as forward acceleration magnitude decreased was primarily attributable to the ankle during early stance and the hip during late stance. The augmentation of power absorption and negative work done by the hip and ankle would therefore suggest that these two joints become increasingly more reliant on the return of elastic strain energy as forward acceleration magnitude decreases and sprinting speed approaches maximal limits.

Our experimental data generally concur with the results from previously published studies investigating maximum acceleration sprinting in humans. Comparisons with existing data can be made from two perspectives. Firstly, previous studies have reported GRF data for maximum acceleration sprinting on an overground track. Recent studies have generated a complete dataset from a single continuous trial using a unique 54 force-plate system (Colyer et al., 2018; Nagahara et al., 2018a,b; Matsuo et al., 2019) or have reconstructed a ‘virtual’ 40 m sprint using data obtained from multiple trials (Morin et al., 2015; Rabita et al., 2015) in a similar

manner to what was done in the present study. Irrespective of the experimental design, collectively these studies found that as speed increases throughout the acceleration phase, braking impulses progressively increase while propulsive impulses progressively decrease, which is consistent with our findings (Fig. 1, Table 1). Moreover, Rabita et al. (2015) found the ratio of forces (averaged across stance phase) decreased from values of  $\sim 40\%$  for the 1st foot contact (excluding values measured from the starting blocks) to values of  $<10\%$  when close to maximum speed. Similarly, our values for the ratio of forces significantly decreased from  $36.99 \pm 4.39\%$  for the high acceleration condition to  $17.22 \pm 2.00\%$  for the low acceleration condition (Table 1). Secondly, previous studies have also reported data describing stance phase lower-limb joint mechanics during maximum acceleration sprinting (Jacobs and van Ingen Schenau, 1992; Johnson and Buckley, 2001; Hunter et al., 2004; Mero et al., 2006; Charalambous et al., 2012; Debaere et al., 2013; Bezodis et al., 2014; Yu et al., 2016; Brazil et al., 2017). Even though most studies to date have only focused on a single discrete region of the acceleration phase (Jacobs and van Ingen Schenau, 1992; Johnson and Buckley, 2001; Hunter et al., 2004; Mero et al., 2006; Charalambous et al., 2012; Debaere et al., 2013; Bezodis et al., 2014; Brazil et al., 2017), it is still possible to make some valid comparisons between data available in the literature and results from the present study. For example, Jacobs and van Ingen Schenau (1992) recorded data from seven elite level male athletes for the 2nd foot contact of maximum acceleration sprinting. They reported peak stance phase



**Fig. 6. Group mean lower-limb joint power plotted across stance phase for the three acceleration conditions.** Joint power data were normalised to body mass. Power generation is positive and power absorption is negative. Stance phase was time normalised from 0% (foot strike) to 100% (toe-off). (A) The hip joint power. (B) The knee joint power. (C) The ankle joint power.



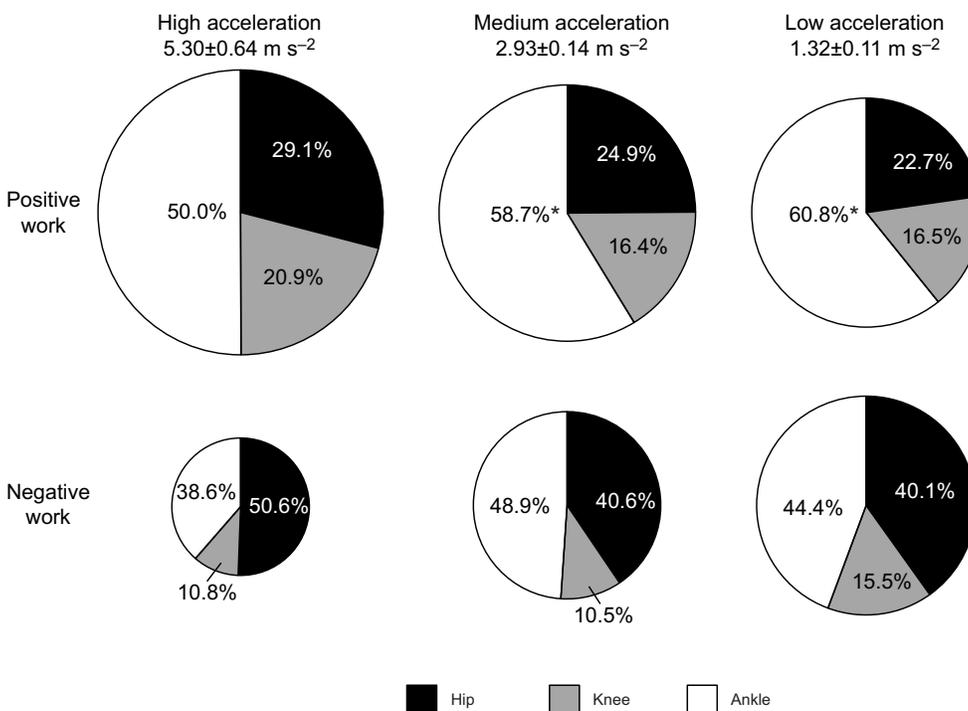
**Fig. 7. Net joint work versus forward acceleration magnitude.** The circles represent data for each foot contact for a single lower limb for all participants ( $N=77$  foot contacts analysed in total). (A) Net work done by the hip joint. (B) Net work done by the knee joint. (C) Net work done by the ankle joint. The red lines show best-fit linear regressions describing the relationship between forward acceleration magnitude ( $x$ ) and net work done by each joint ( $y$ ).

knee and ankle joint moments of  $1.80\pm 0.17$  and  $3.15\pm 0.10$  N m kg<sup>-1</sup>, respectively. These data compare favourably with equivalent peak joint moments for the high acceleration condition from the present study of  $1.63\pm 0.59$  and  $3.20\pm 0.34$  N m kg<sup>-1</sup> (Table 2). More recently, Brazil et al. (2017) investigated lower-limb joint mechanics during maximum acceleration sprinting where data were recorded from 10 elite male athletes for the 1st foot contact following the starting blocks. Along with a range of other variables, they calculated the proportional contribution from each joint to the summed amount of positive work done by the lower limb. Proportional contributions were found to be 31%, 26% and 43% for the hip, knee and ankle, respectively. Again, these data are consistent with results from the present study; specifically, we found the proportional contributions to the summed amount of positive work done by the lower limb for the high acceleration condition to be 29.1%, 20.9% and 50.0% for the hip, knee and ankle, respectively (Fig. 8, top). Given that our data are consistent with previous studies, we therefore have much confidence in the validity of our experimental procedures.

#### Lower-limb joint mechanics during maximum acceleration sprinting versus steady-state running

Many previous studies exploring the effect of running speed on lower-limb joint mechanics in humans have done so by comparing data across a range of discrete constant (i.e. steady-state) running speeds (Ae et al., 1987; Arampatzis et al., 1999; Belli et al., 2002; Schache et al., 2011, 2014, 2015). Interestingly, studies adopting this type of experimental design have reported some alternative findings regarding the behaviour of the hip, knee and ankle with increasing running speed relative to what we observed in the present study. When the objective of the task changes from maintaining a constant speed to increasing the body's forward kinetic energy as quickly as possible, we discovered that mechanical function is adjusted at all three major lower-limb joints to some extent.

Using a steady-state running protocol, we previously found that the amount of positive work done by the hip during stance gradually increased from  $0.06\pm 0.04$  to  $0.20\pm 0.13$  J kg<sup>-1</sup> when speed progressed from  $2.08\pm 0.13$  to  $6.99\pm 0.09$  m s<sup>-1</sup>, before increasing



**Fig. 8. The proportional contributions of each joint to the summed amount of positive (top) and negative (bottom) work done by the lower limb.** Note that the total area of each pie chart is scaled such that it represents the summed amount of work done by the lower limb relative to the other conditions (i.e. greater area equals more work done). The asterisk indicates a significant difference with respect to the ankle's proportional contribution to the summed amount of positive work done by the lower limb for the high acceleration condition.

more dramatically to  $0.51 \pm 0.17 \text{ J kg}^{-1}$  at a speed of  $8.95 \pm 0.70 \text{ m s}^{-1}$  (Schache et al., 2015). In contrast, here we found positive work done by the hip during stance to not only be amplified in magnitude but also show the opposite response with increasing running speed. Positive work done by the hip averaged  $0.93 \pm 0.41 \text{ J kg}^{-1}$  for the high acceleration condition and it decreased to  $0.50 \pm 0.23 \text{ J kg}^{-1}$  for the low acceleration condition (Table 2). The greater amount of positive work done by the hip during maximum acceleration sprinting was largely a by-product of the increased hip extensor load during early stance. For the high acceleration condition, the trunk was inclined forwards by  $\sim 60$  deg with respect to the vertical (Fig. 3A). This orientation ensured that the net GRF vector was situated anterior to the hip joint for as long as possible during stance (e.g. note in Fig. 4A how acceleration condition affects the point during stance when the polarity of the hip joint moment curve switches from positive to negative), thereby maximising the capacity of the hip joint to aid with forward propulsion.

Some noteworthy differences in knee joint mechanics were also apparent when comparing results from the present study with those obtained from studies examining steady-state running conditions. For example, the joint power profile at the knee for steady-state running typically displays a sinusoidal pattern (irrespective of running speed), with a period of power absorption during early stance that is immediately followed by a period of power generation during late stance (Arampatzis et al., 1999; Belli et al., 2002; Schache et al., 2011, 2015). Net work done by the knee during stance was therefore found to remain relatively invariant across a broad range of steady-state running speeds (Schache et al., 2015). In contrast, for the high acceleration condition in the present study, we found the knee to be flexed at foot-strike and then it continuously extended throughout stance (Fig. 3C), with a complete absence of any period of power absorption or negative work done by the knee during early stance (Fig. 6B). Moreover, the net work done by the knee was found to display a positive linear relationship with forward acceleration magnitude (Fig. 7B). These findings are probably attributable to a change in the mechanical function of the knee joint. During the stance phase of steady-state running, knee joint mechanics may be described as resembling a spring with a period of negative work immediately preceding a period of positive work (Rubenson et al., 2011), whereas here we found knee joint mechanics to be more akin to a motor when forward acceleration magnitude was highest.

Finally, differences in ankle joint mechanics can be identified when comparing results from studies examining steady-state running conditions versus those from the present study for maximum acceleration sprinting, with differences being similar to what we have described above for the knee. For steady-state running, the joint power profile at the ankle (like the knee) is characterised by a period of power absorption during early stance followed by a period of power generation during late stance (Arampatzis et al., 1999; Belli et al., 2002; Schache et al., 2011, 2015). In the present study, we observed ankle joint mechanics to display a definite bias towards power generation and positive work when forward acceleration magnitude was highest (Table 2), although note that (unlike the knee) a small amount of power absorption and negative work still occurred at the ankle during early stance even for the high acceleration condition (Fig. 6C). Net work done perhaps best encapsulates the differences in ankle joint mechanics between running conditions. We previously calculated net work done at the ankle during stance for five different steady-state running speeds varying from  $2.08 \pm 0.13$  to  $8.95 \pm 0.70 \text{ m s}^{-1}$  (Schache et al., 2015): it increased in magnitude slightly with faster

running but never exceeded  $0.9 \text{ J kg}^{-1}$ . In the present study, we found net work done at the ankle to display a strong positive linear relationship with forward acceleration magnitude (Fig. 7C), having an average magnitude of  $1.19 \pm 0.14 \text{ J kg}^{-1}$  for the high acceleration condition (Table 2).

#### How do our results for humans compare with equivalent data for animals?

Several studies have measured lower-limb joint mechanics during acceleration for various animals (Roberts and Scales, 2004; McGowan et al., 2005; Williams et al., 2009). Whilst data from these studies can be compared with results from the present study in order to understand how lower-limb joint mechanics differ for humans versus bipedal and quadrupedal animals, it is important to note some methodological distinctions amongst the studies. It is difficult to motivate animals in an experimental setting to continuously accelerate with maximal exertion to reach their peak speed as quickly as possible. Hence, prior animal-based studies have either captured data for the initial few foot contacts for accelerations performed at a variety of intensities (Roberts and Scales, 2004; McGowan et al., 2005), or captured data for a larger number of foot contacts but only for accelerations performed at a submaximal intensity (Williams et al., 2009). Hence, it is likely that the animals never attained their maximal locomotion speed during data collection in any of these studies. Such methods differ somewhat from the present study, where all trials involved maximal exertion and data were captured not only for the beginning of the acceleration but also at the end when participants were close to their peak sprinting speed. Thus, we were able to analyse a near full spectrum of forward acceleration magnitudes during sprinting for humans.

Keeping these methodological differences in mind, some interesting outcomes were revealed when comparing the main findings amongst studies. For example, Williams et al. (2009) had six racing greyhounds perform submaximal accelerations at a range of intensities. They measured the ratio of impulses by dividing the impulse of the vertical GRF by the net impulse of the horizontal GRF (opposite to the present study) and found it to approach an asymptote (or minima) of around two with increasing forward acceleration magnitude. In other words, the magnitude of the net impulse of the horizontal GRF never exceeded 50% of the impulse of the vertical GRF. This result is similar to what we observed in the present study for humans (Fig. 2). Williams et al. (2009) proposed that the limit on the ratio of impulses with increasing forward acceleration magnitude depended upon the coefficient of friction, and hence it primarily reflected the amount of grip between the foot and the ground. Whilst this relationship is true (we all know how difficult it is to accelerate forwards when standing on a slippery surface), participants in the present study ran on an indoor synthetic track wearing their usual running spikes. Thus, we expect that grip between the foot and the ground was optimised in this situation. We therefore suggest that a ratio of impulses of  $\sim 50\%$  (net impulse of the horizontal GRF divided by the impulse of the vertical GRF) could be close to a 'physiological' limit for what can be achieved by humans during maximum acceleration sprinting without the use of starting blocks.

One biomechanical variable that was calculated in all studies and can be readily compared across species is the net work done at each joint versus forward acceleration magnitude. For humans, we found strong linear relationships to exist between net work done and forward acceleration magnitude for all three joints, with the slope of the regression line being steepest at the hip and ankle (Fig. 7). Our

results compare favourably to what was reported for other bipedal animals. For example, Roberts and Scales (2004) investigated joint mechanics in wild turkeys and found significant linear relationships to exist between net work done and forward acceleration magnitude only at the hip ( $R^2=0.64$ ) and ankle ( $R^2=0.84$ ), with the slope of the regression line at the ankle (0.192) being slightly steeper than that at the hip (0.154). Similarly, McGowan et al. (2005) investigated joint mechanics in tammar wallabies and found significant linear relationships to exist between net work done and forward acceleration magnitude at the hip ( $R^2=0.35$ ), ankle ( $R^2=0.83$ ) and metatarsophalangeal joint ( $R^2=0.39$ ), with the relationship at the metatarsophalangeal joint being negative rather than positive. The slope of the regression line was steepest at the ankle (0.302). These findings together with those from the present study suggest that for bipedal locomotion the hip and ankle are especially important for modulating work when accelerating. In comparison, Williams et al. (2009) investigated lead and trail hindlimb joint mechanics in racing greyhounds. They found significant linear relationships to exist between net work done and forward acceleration magnitude at the knee ( $R^2=0.28$ ) and ankle ( $R^2=0.41$ ) for the lead hindlimb only. Such findings would suggest that some fundamental differences in joint mechanics do exist between bipedal and quadrupedal locomotion.

### Limitations

This study was associated with a number of limitations. First, we used an inverse-dynamics approach to quantify lower-limb joint mechanics. Whilst a similar approach was taken by many previous studies exploring locomotor biomechanics in humans and various animals, we do appreciate that inverse-dynamics-based analyses offer limited insight regarding many important elements of skeletal muscle function, such as co-contraction between antagonistic muscles, force distribution amongst synergistic muscles, and the relative contribution from muscle fibres and tendons to joint power and work. Furthermore, because biarticular muscles (e.g. hamstrings, rectus femoris, gastrocnemius) have the capacity to transfer power between the lower-limb joints (Jacobs et al., 1996), changes in power and work at a given joint do not necessarily reflect changes in the power output of muscles that cross that joint.

Second, instrumentation constraints meant that experimental data for the acceleration phase of the overground sprint task were collected in stages (six different starting locations on the running track per participant). This protocol is similar to that successfully utilised by previous researchers (Cavagna et al., 1971; Morin et al., 2015; Rabita et al., 2015). Ideally, data for the entire acceleration phase would have been collected within a single continuous trial, but such a scenario for overground sprinting would necessitate a calibrated measurement space capable of recording both GRF data and marker trajectories that extended beyond 40 m in length. Because participants were instructed to accelerate with maximal effort for all trials, we believe that our data closely resemble what would be expected for a single continuous effort. For example, horizontal GRF data for a single representative participant for 10 consecutive ipsilateral foot contacts are plotted in Fig. S2. These data match what has recently been reported for a single continuous trial using a laboratory containing 54 force plates mounted in series (Colyer et al., 2018). We are therefore confident that the process of building the acceleration phase from multiple trials had no adverse impact upon our results.

Third, we did not quantify lower-limb joint mechanics for either the front or rear legs in the starting pose. Using novel force instrumented starting blocks, Brazil et al. (2017) found that the total net work done by the lower-limb joints (hip, knee, ankle) was

1.7-fold greater for the front leg in the starting blocks compared with the 1st foot contact after leaving the starting blocks. Thus, considerable work is done by the lower-limb joints in the starting pose, especially for the front leg, implying that the high acceleration condition in the present study may not have been the highest in terms of maximum forward acceleration magnitude.

Fourth, we modelled the foot as a single segment, consistent with many previous inverse-dynamics-based investigations of human locomotion (Jacobs and van Ingen Schenau, 1992; Belli et al., 2002; Roberts and Belliveau, 2005; DeVita et al., 2007; Rubenson et al., 2011; Farris and Sawicki, 2012; Pires et al., 2014). Previous studies have calculated the power and work done by the metatarsophalangeal joint during sprinting and have found it to make a negligible contribution to the positive work done by the lower limb (Stefanyshyn and Nigg, 1997; Bezodis et al., 2014). Thus, we do not believe our modelling simplification adversely affected our main conclusions.

Fifth, data were collected from a relatively small sample of young ( $\leq 34$  years) sub-elite level track and field athletes. Whilst our cohort proved capable of unveiling some novel and interesting relationships (e.g. Fig. 5), it is possible that lower-limb joint mechanics during maximum acceleration sprinting could be influenced by factors such as ability (Rabita et al., 2015) and ageing (Kulmala et al., 2014). Future research is therefore required to further explore these possibilities.

Sixth, the primary outcome measures of interest in the present study were derived using non-invasive skin marker-based motion capture and thus were susceptible to various errors such as misaligned joint axes of rotation as well as movement of the tracking markers relative to the underlying bone due to the interposing soft tissues (skin, fatty tissue, muscle, etc.). However, we followed a previously published protocol that incorporated several strategies to specifically minimise these types of errors (Schache et al., 2011). Furthermore, given the within-participant repeated measures design of the present study, we anticipate that such errors had minimal impact on our main findings.

### Conclusion

The present study explored how humans adjust the stance phase mechanical function of their major lower-limb joints (hip, knee, ankle) during maximum acceleration sprinting. We conclude that the hip and especially the ankle represent key sources of positive work that can help meet the objective of maximising the body's forward kinetic energy when rapidly accelerating from a stationary position.

### Competing interests

The authors declare no competing or financial interests.

### Author contributions

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### Supplementary information

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